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ATLANTIC COAST MIGRATIONS OF AMERICAN SHAD

By GERALD B. TALBOT AND JAMES E. SYKES

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ABSTRACT

The returns from 17,508 American shad (*Alosa sapidissima*) tagged at various places along the Atlantic coast over a period of 19 years have been used to study the migrations of this fish. Thirty-nine percent of these tags were recovered. These recoveries disclosed that after spawning, adult shad from Chesapeake Bay to the Connecticut River migrate northward and spend the summer and fall in the Gulf of Maine. Canadian shad migrate southward to spend the same period in the Gulf of Maine. There is only slight evidence as to where shad spend the winter months, but it appears that they are scattered along the Middle Atlantic area, probably in deep water, for beginning in January or February as the spawning season approaches they move inshore and shad which spawn from Georgia to the St. Lawrence River are caught from North Carolina to Long Island. Those not caught migrate either north or south to their native streams and spawn, repeating this cycle each year if they escape natural and fishing mortalities. The young shad leave their native streams in the fall; probably spend the winters in the Middle Atlantic area, migrate to the Gulf of Maine each summer along with the adults; and when mature return to their native streams to spawn. Those shad that spawn in streams south of Chesapeake Bay and particularly south of North Carolina die after spawning. How or by what mechanism shad and other anadromous fishes are guided in their migrations has not yet been satisfactorily determined.

ATLANTIC COAST MIGRATIONS OF AMERICAN SHAD

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The study of fish migrations has long intrigued many persons. Much of the early work was inspired by scientific curiosity or undertaken as a hobby by wealthy owners of riparian rights. More recently, however, knowledge of fish migrations has been necessary for the intelligent management of some species, since many fisheries depend on congregations of migrating fish. This is particularly true of the American shad (*Alosa sapidissima*) of the Atlantic coast.

Very little has been published concerning the migrations of shad. Vladykov (1950, 1957) studied the migrations of tagged shad in the St. Lawrence River in Canada, and Vladykov and Wallace (1937: p. 64) mentioned one distant recovery of a shad tagged in Chesapeake Bay. Most of the work on anadromous fish migrations has been undertaken on the several species of salmon and much of it has revolved around three problems: (1) Do anadromous fish move long distances from the stream where they were spawned; (2) if so, do they find their "home" stream again when they become mature and return to fresh water to spawn; and (3) if they return to their home stream, how or by what mechanism do they find it.

Rutter (1902: p. 121) maintained that it was "incredible that the salmon remember their native stream," and asserted that if they did return to their native stream it was only because they never did stray from its influence; therefore, the salmon were attracted by that stream when ready to return to fresh water. Huntsman (1937) has been a proponent of Rutter's theory and stated, "It would seem that if a fish happened to get very far from this zone of the river influence. . . . It may be said to be 'lost.'" Others, however, have shown that salmon migrate long distances in the sea and yet return in a great majority of the cases to their native rivers (Calderwood 1937: p. 207; Clemens, Foerster, and Pritchard, 1939: p. 51; Davidson 1937: p. 55; Rich 1937a: p. 477, 1937b: p. 122, 1939: p. 45).

Very little has been determined as to how anadromous fish find their way back to their native rivers from great distances in the sea and then up the various tributaries to their native streams. Ward (1921a, 1921b, 1939a: p. 1, 1939b: p. 60) studied sockeye salmon of the Copper River in Alaska, and the Skagit River in Washington and concluded that when migrating up a river and presented with a choice at the fork of a stream these salmon always choose the one with the cooler water. Powers (1939), Powers and Clark (1943), and Powers and Hickman (1928) attributed the direction taken by sockeye salmon to gradients of salinity in the sea and to gradients of carbon dioxide tension in the sea and in the rivers.

In 1939, however, Scheer (p. 426) pointed out that—

> Although the suggestions made by these writers are of some value in indicating possibilities, neither has taken into consideration the fact that a run of fishes, whether in the sea or in a river, may divide, some passing into one river or tributary while others continue on their previous course.

This is particularly true in a large river system such as the Fraser where Talbot (1950) has shown that several races of sockeye salmon are migrating upstream at the same time, each passing into its own system and tributary. That each of these is a separate race has been pointed out by Thompson (1945).

More recently Collins (1952), working with *Pomolobus pseudoharengus* and *P. aestivalis*, has shown that when given a choice the majority of these fish entered the warmer channel when the

Note—Approved for publication, June 27, 1957. Fishery Bulletin 142.

temperature difference continuously exceeded 0.5° C., or the channel where the free CO_2 was lowest when the difference exceeded 0.3 p.p.m. Also, Hasler and Wisby (1951), Wisby and Hasler (1954), and Hasler (1954) have shown by careful experimentation that fishes have a remarkable olfactory sense by which they can detect a difference between streams, and that this may explain the salmon's ability to return to its parental stream. While these experiments prove without doubt that fish can differentiate between odors, temperatures, et cetera, they do not explain how the fish find their way to their home rivers from great distances in the sea, or how they find their way upstream in a large river system to the area where it is conceivable that their senses of differentiation might begin to influence their choice of tributaries, as mentioned by Scheer.

Concerning shad migrations, Stevenson (1899: p. 106) stated—

> it was formerly considered that the entire body of shad wintered in the South and started northward in a vast school at the beginning of the year . . . sending a detachment up each successive stream, this division, by a singular method of selection, being the individuals that were bred in those respective streams, the last portion of the great school entering the Gulf of St. Lawrence. ". . . the present theory [1899] is that the young shad hatched out in any particular river remain within a moderate distance off the mouth of that stream until the period occurs for their inland migration, and that the schools of fish are generally distributed off the coast at all times, entering the rivers as soon as the temperature of the water is suitable.

Bigelow and Schroeder (1953: p. 108) partially, at least, subscribe to the latter theory for they state that, "Probably the shad of the year winter near the mouths of their parent streams; the larger sizes somewhat farther out and deeper." That some shad do migrate long distances has been pointed out by Bigelow and Schroeder quoting from unpublished work by the U. S. Fish and Wildlife Service, and work by Vladykov and Wallace (1938) and Vladykov (1950).

This paper presents data from many shad tagging experiments carried out by the United States Fish and Wildlife Service during the past 19 years which illustrate the migrations of this species. The work was completed as part of an investigation of Atlantic coast shad carried out by the Service as the primary research agency of the Atlantic States Marine Fisheries Commission.

The tagging programs used as the basis of this paper were undertaken by many biologists of the United States Fish and Wildlife Service and its predecessor, the United States Bureau of Fisheries. Biologists from the New York Conservation Department, the Chesapeake Biological Laboratory, and Virginia Fisheries Laboratory have also assisted and furnished equipment on many occasions. The assistance of these agencies and biologists is gratefully acknowledged.

LIFE HISTORY

Shad are the largest members of the herring family in the United States. They are anadromous, spawning in the spring of the year in streams from the St. Johns River in Florida to the St. Lawrence River in Canada. The spawning migrations begin earliest in the south (November in the St. Johns River) and are progressively later in northward rivers depending upon the latitude. The eggs are about 3 millimeters in diameter, are nonadhesive, and are deposited loosely in the water. After absorbing water, the eggs sink to the river bottom and are carried along by the current. The number of eggs produced each season per female averages about 250,000, and not 25,000 or 30,000 as is so often quoted in the literature (U. S. Commission of Fish and Fisheries, 1898; Lehman 1953). The eggs hatch in 6 to 8 days at 17° C. The young live in the rivers during the summer and usually migrate to sea in the fall of the same year, at which time they are 3 to 5 inches in length. Shad mature and return to the rivers to spawn 3 to 6 years later—most return at 4 or 5 years of age. After spawning, if they survive natural and fishing mortalities, they return to the sea. The following year they again return to fresh water to spawn, and at this time are called "repeaters." The age of shad and number of times they spawn can be determined from their scales (Cating 1953).

TAGGING PROGRAMS

The returns from tagging 17,508 shad at many locations along the eastern coast of the United States during the years 1938 through 1956 were used in this study. These are shown in table 1. Prior to 1950 the tagging programs were of a

mited nature, carried out over a short period ach year, usually in the ocean or bays, for the urpose of determining either the migration pat-erns of shad or the rivers to which shad were eturning when intercepted by commercial fishing ear. Beginning in 1950, most of the tagging was carried out in rivers during the entire spawning season, primarily for the purpose of estimating population size and related data. Those surviving fishing and natural mortality returned to the ocean and later, when caught, gave evidence of migration patterns.

TABLE 1.—*Shad tagged and tags recovered, 1938–56*

(1) Place of tagging	(2) Date of tagging	(3) Number of fish tagged	Number of tags recovered— (4) Near tagging site	(5) Before or during spawning	(6) After spawning	(7) In following springs [1]	(8) Miscellaneous [2]
Maine:							
Mount Desert Rock	Aug. 28, 1947	242		29			
Pinkham Bay	Aug. 23–24, 1948	201		10			1
Pleasant River	Aug. 27 to Sept. 10, 1948	158		4			
Connecticut:							
Connecticut River:							
Saybrook	Apr. 14 to July 9, 1951	1,482	408	2	1	24	
Holyoke Dam	June 22, 1954	100				1	
Holyoke Dam	June 1–30, 1956	960	175		1		
New York:							
Fire Island	Apr. 12–22, 1946	97		35			
Fire Island	June 10–19, 1946	101		13	1		
Hudson River	Apr. 23 to June 16, 1950	1,289	356		8	160	12
Hudson River	Apr. 3 to June 9, 1951	2,006	718		7	52	8
Staten Island	Apr. 4 to May 21, 1956	1,054	75	402	1		
New Jersey coast:							
Sandy Hook	Apr. 22–25, 1938	146	5	107	3		
Sandy Hook	Apr. 25–26, 1939	240	4	97			1
Belford	Apr. 16 to May 1, 1940	319	43	94			
Sandy Hook	Apr. 13–14, 1942	220	17	57	1		
Belford	Apr. 22, 1943	100	3	29	1		2
Sandy Hook	Apr. 19, 1944	104	5	22			3
Belford	Apr. 26 to May 3, 1945	85	1	15			
Seaside Park	Apr. 19–20, 1945	126	6	34	1		6
Sandy Hook	Apr. 22–25, 1946	176	3	19			5
Beach Haven	Mar. 28 to May 22, 1956	943		292	4		
Point Pleasant	Apr. 19 to May 23, 1956	962	2	377	4		
Maryland–Virginia:							
Chesapeake Bay:							
Little Creek, Va	Apr. 20, 1939	338	182		2		
Little Creek, Va	Mar. 22 to Apr. 15, 1940	300	143	15			
Watts Island, Va	Apr. 2–8, 1940	118	74	2			1
Horn Harbor, Va	Mar. 27 to Apr. 10, 1940	125	84	2			
Buckroe Beach, Va	Mar. 21 to Apr. 11, 1940	242	148	2			
Cedar Point, Governors Run, Tilghman Island, Md.	Apr. 16 to May 5, 1941	229	137	1	1		
Watts Island, Va	Apr. 16, 1941	103	56	3	1		
Buckroe Beach, Va	Apr. 9, 1941	100	41	4			
New Point, Va	Apr. 21, 1942	97	43	1			
New Point Light, Va	Apr. 1, 1943	101	30	1			
Potomac River	May 22, 1950	63	8		1		
Potomac River	Mar. 13 to May 28, 1952	321	188	1	2		2
James River	Mar. 1 to Apr. 30, 1952	374	264	6			
Little Creek, Va	Mar. 18 to May 10, 1952	1,395	509	63	5		
Susquehanna Flats	Apr. 10 to May 27, 1952	449	257		2		4
Solomons, Md	Apr. 2 to June 3, 1952	420	226	2			
NorthCarolina: Neuse River	Jan. 7 to Apr. 14, 1953	377	222	1			3
South Carolina: Edisto River	Feb. 15 to Apr. 15, 1955	128	16				
Georgia: Ogeechee River	Feb. 3 to Apr. 15, 1954	235	133				
Florida: St. Johns River	Dec. 15, 1952 to Apr. 7, 1953	882	188				2
Total		17,508	4,770	1,740	49	237	50

[1] Shad tagged on spawning ground.
[2] Tags recovered in markets, homes, et cetera; no data available on area or date of recapture of fish.

In almost all cases the fish were obtained for tagging from commercial fishing gear. In Maine, shad were captured in weirs and purse seines. On the New York–New Jersey coast, Chesapeake Bay, and the Neuse River in North Carolina, shad were captured by pound nets, and in the latter two locations by haul seines also. Practically all the other fish caught in rivers were from gill nets except in the St. Johns River, Florida. Here, shad are also caught in large numbers by a special-type haul seine (locally termed "shad nets") operated by power boats. In a few cases, shad were captured by the tagging crews using gill nets and haul seines.

Fish in good condition were selected as the nets were emptied. In most cases, the fishermen would

cooperate by slowing down their operations so that the fish for tagging were out of the water a minimum of time. Where this was not possible the fish were placed in tubs or tanks of fresh water until tagged and released. Most of the fish were marked with Petersen disk tags consisting of two celluloid disks, held in place, one on each side of the back just below the dorsal fin, by a nickel pin that passes through the fish. Strap tags (modified cattle ear tags) were affixed to the gill covers of a few shad, and also a few fish were marked with cheek tags (bachelor-button-type), which consist of a plastic disk held to the outer surface of the gill cover by a rivet that passes through the gill cover (fig. 1). A return legend and serial number were printed on each tag for identification purposes and a reward was paid as an incentive to the finder to return the tag.

Some tagging experiments (including all internal belly tags) are not reported in this paper, since there either were no returns, no data with returns, or the fish were recaptured shortly after tagging near the locality of tagging and, therefore, did not illustrate migration. All of the internal belly tags returned (5 percent of the fish tagged) were from markets, homes, et cetera, or were found when the

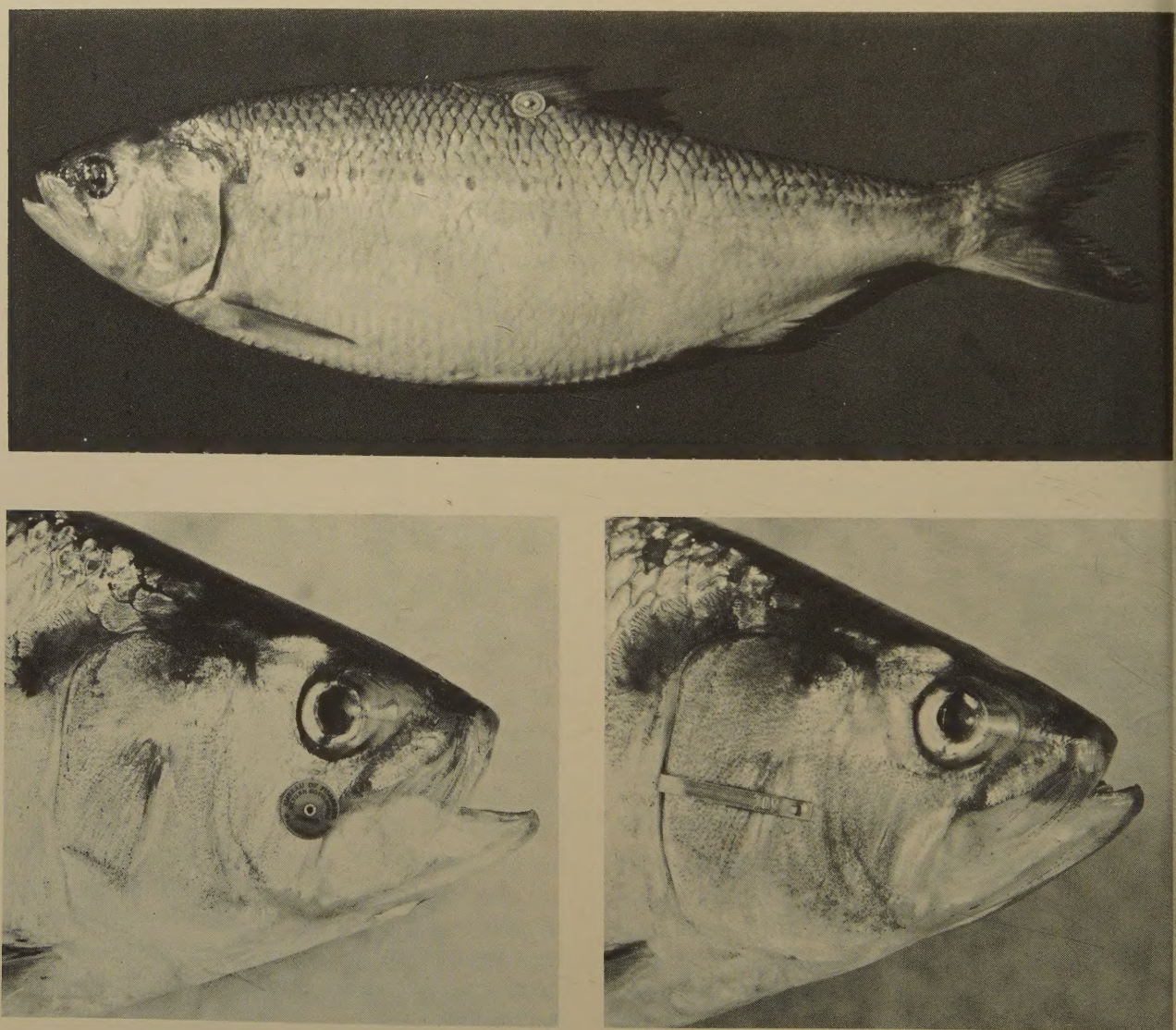

FIGURE 1.—Upper: Male shad tagged with Petersen disk tag. Lower left: Shad with cheek tag. Lower right: Shad with strap tag.

fish were being cleaned; thus, the place of recapture was doubtful in most cases.

All of the shad were tagged during spring spawning runs with the exception of those tagged in Maine during August and September. A total of 6,846 tags were recovered from these experiments. Petersen disk tags gave the highest percentage of returns (40 percent), while only 11 percent of the strap and 8 percent of the cheek-type tags were recovered. The low recovery of the tags applied to the gill covers probably resulted because they are not easily seen or because they are more easily detached from the fish than are the Petersen disk tags. In some cases Petersen disk tags have been shown to cause the fish to be more readily entangled in gill nets, and this may be partly responsible for the higher recapture rate of fish bearing this type of tag.

ANALYSIS OF TAG RETURNS

To facilitate analysis of the tagging, the 6,846 returns from the many tagging programs were classified in table 1 as follows: (1) Recoveries near the tagging site (col. 4); (2) recoveries before or during spawning, usually March through May (col. 5); (3) recoveries after spawning, June 1 or June 15 through November (col. 6); (4) recoveries of those fish tagged on the spawning ground and captured the following years during the spring (col. 7); and (5) miscellaneous, including returns from markets, homes, et cetera (col. 8), where it was impossible to determine the place and/or date of recapture. All tags recovered from the tagging experiments were assigned to the appropriate category (table 1). Tag recoveries in the first two categories were made during the same period, but only those showing movement away from the tagging site were listed as tag recoveries "before or during spawning." Tags recovered near the tagging site were not used in this study since they showed no migration, but they were listed in column 4 so that all recoveries would be accounted for.

Of the tags affixed on the spawning grounds in the Hudson and Connecticut Rivers, no difficulty was experienced in separating those recovered before or during spawning (col. 5) from those recovered after spawning (col. 6). In this case, if the tags were recovered outside the river, they were considered as having been recovered after spawning. A few tags recovered from fish tagged on the coast of New Jersey and in the Chesapeake Bay area were not so easily classified, since it was not known exactly where these fish had spawned. Shad tagged at these places were recovered from spawning areas in the Chesapeake and Delaware Bays, the Hudson and Connecticut Rivers, and in Canadian streams. However, spawning in all streams south of Long Island is virtually completed by May 31, while spawning in the Connecticut River is usually completed by June 15. In the few doubtful cases, if the tags were recovered in the ocean after May 31 south of Long Island or after June 15 off Massachusetts, Maine, or Canada, they were arbitrarily classified as having been taken after spawning. Therefore, using these criteria, a few errors in classification may have resulted, since shad tagged in Chesapeake Bay or on the coast of New Jersey and recaptured between Long Island and Canada after June 15 were classified as captured after spawning, but they could have been on their way to spawn in streams in Maine or Canada, where spawning occurs in June and even as late as July. These cases were few, and even if improperly classified they still help to illustrate the migration pattern of shad at this time of year.

Five percent of the tags used in our study of shad migrations were recovered 1 to 4 years after tagging. Of these, 55 percent were recovered on the spawning grounds and listed in column 7 of table 1. The others are listed under columns 5 or 6, regardless of year of recovery. In other words, a tag recovered from near the tagging site 1 or more years after tagging was classified under column 4. A tag recovered in the ocean after 1 or more years was classified under column 5 or column 6, the same as if it were recovered the year the fish was tagged. This was necessary since there was no way to determine where the fish bearing these tags had been during the intervening periods. The assumption in these cases was that the fish were repeating a migration pattern that they followed each year and, therefore, were properly classified.

The returns from the Gulf of Maine tagging, listed in column 5, were analyzed under a heading separate from the other tags in this column. The Maine tagging was carried out in August and September and illustrates a migration pattern different from the other tag recoveries in column 5,

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which were tagged during the spring months. The tag recoveries from Maine and those listed in table 1, columns 4, 5, and 6 are discussed in the following sections.

TAG RECOVERIES BEFORE AND DURING SPAWNING

In this group are fish recaptured on their way to the spawning grounds or on the spawning grounds that were tagged in the spring (mostly March through May) off Fire Island, New York, and the coast of New Jersey, in Chesapeake Bay, and at the mouth of the Neuse River in North Carolina. Recoveries in this group from tagging conducted at the first two locations are shown graphically in figure 2, and those from Chesapeake Bay and the Neuse River in figure 3. The broken lines showing the paths of migration in these and the following figures are not intended to give the exact routes followed by the migrating shad, but merely to indicate the tagging and recovery areas.

The tagging near Fire Island was carried out in two periods during 1946 (table 1). Those shad tagged from April 12 to 22 were mostly recaptured in the Connecticut River (26 fish), while only nine (included in the 20 shad in fig. 2) were recovered in the Hudson River. Those fish tagged from June 10 to 19 were mostly spawned-out shad from the Hudson River, for only 1 tag was recovered from the Connecticut River that year, while during the shad run of the following year 11 fish were recaptured from the Hudson River and none was recovered from the Connecticut River.

Tag recoveries indicate that most of the shad tagged on the coast of New Jersey and Staten Island were bound for the Hudson (1,377 fish recaptured) and Connecticut Rivers (120 fish recaptured) as shown in figure 2. A few were recaptured in Delaware Bay and in the spawning areas of the Maurice River, a tributary to the bay. Some also were recaptured in Chesapeake Bay and tributaries, while a few were recaptured early in the season en route to, or in, Canadian rivers. The recapture of a shad tagged in June off Fire Island was made in North Carolina the following spring.

Most of the shad tagged in Chesapeake Bay were recaptured in the near vicinity either in the bay or its tributaries, where they spawn (table 1, col. 4). The same is true of those shad that spawned in the Neuse River, where all but one of the recaptures were made either in this river or in neighboring waterways. The tagged shad which did leave the vicinity of tagging and were recovered before or during the spawning season are shown in figure 3. As with those fish tagged on the coast of New Jersey and off Fire Island, some of the shad tagged in the Chesapeake Bay area migrated long distances during this period and spawned in widely separated streams from South Carolina to Canada.

TAG RECOVERIES AFTER SPAWNING

All tags that were affixed in the Hudson and Connecticut Rivers, along the coast of New Jersey, and in Chesapeake Bay, and recovered after spawning in these areas was completed, are plotted in figure 4. Tags recovered during this period indicated a shad migration in the ocean northward from the tagging area. Recoveries off Long Island of fish tagged in the Hudson River were made from June 5 through June 25. Fish tagged in Chesapeake Bay were recaptured off Long Island from June 9 through June 17, while shad tagged on the coast of New Jersey, and which spawned predominantly in the Hudson River as previously shown, were recaptured off Long Island between June 11 and 26.

The earliest recapture off Massachusetts was on June 22 of a shad tagged at the mouth of Chesapeake Bay on April 14, and the earliest recapture in Maine was July 6 of a shad tagged in Chesapeake Bay on May 21. The earliest recovery in Canada was on July 9 near the mouth of the St. Johns River, New Brunswick. This fish was tagged off New Jersey on April 25.

Tags were recovered off Massachusetts during the months of June, July, and August, and in October and November, while in Maine, New Brunswick, and Nova Scotia, they were recovered only during the months of July, August, and September. These records indicate that the recoveries of tagged fish in June, July, and August may have been made as the shad migrated past Massachusetts on their way north to Maine and Canadian waters, while the October–November recoveries were made as the shad were on their return trip south.

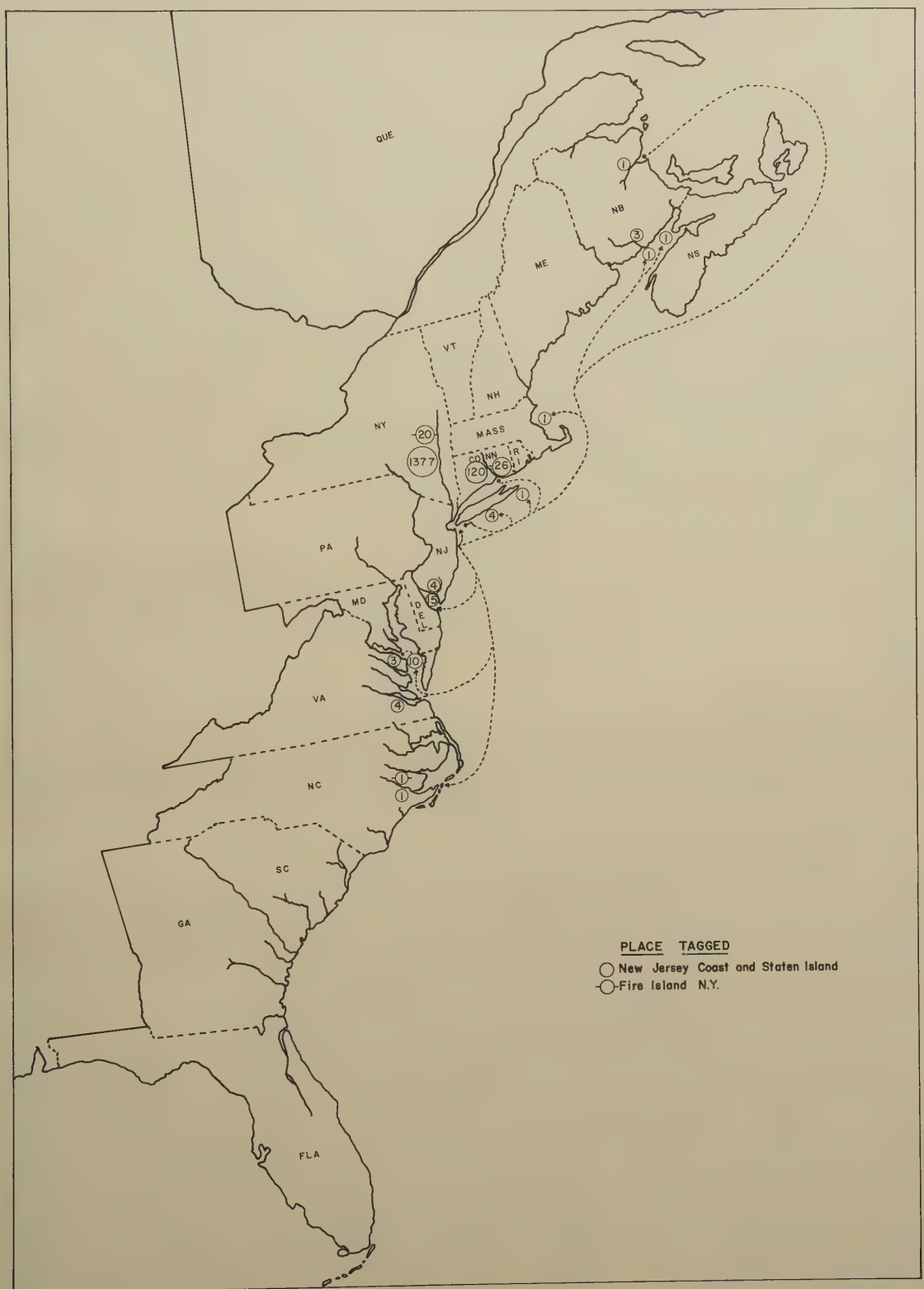


FIGURE 2.—Tags recovered before or during the spawning period (before June 1 south of Long Island and before June 15 off Massachusetts, Maine, and the Canadian Provinces) which were affixed at Fire Island and Staten Island, New York, and along the New Jersey coast during the period March through June. (The broken lines connect place of tagging with place of recapture, but do not necessarily show the migration route. The figures in circles indicate the number of tags recovered in each locality.)

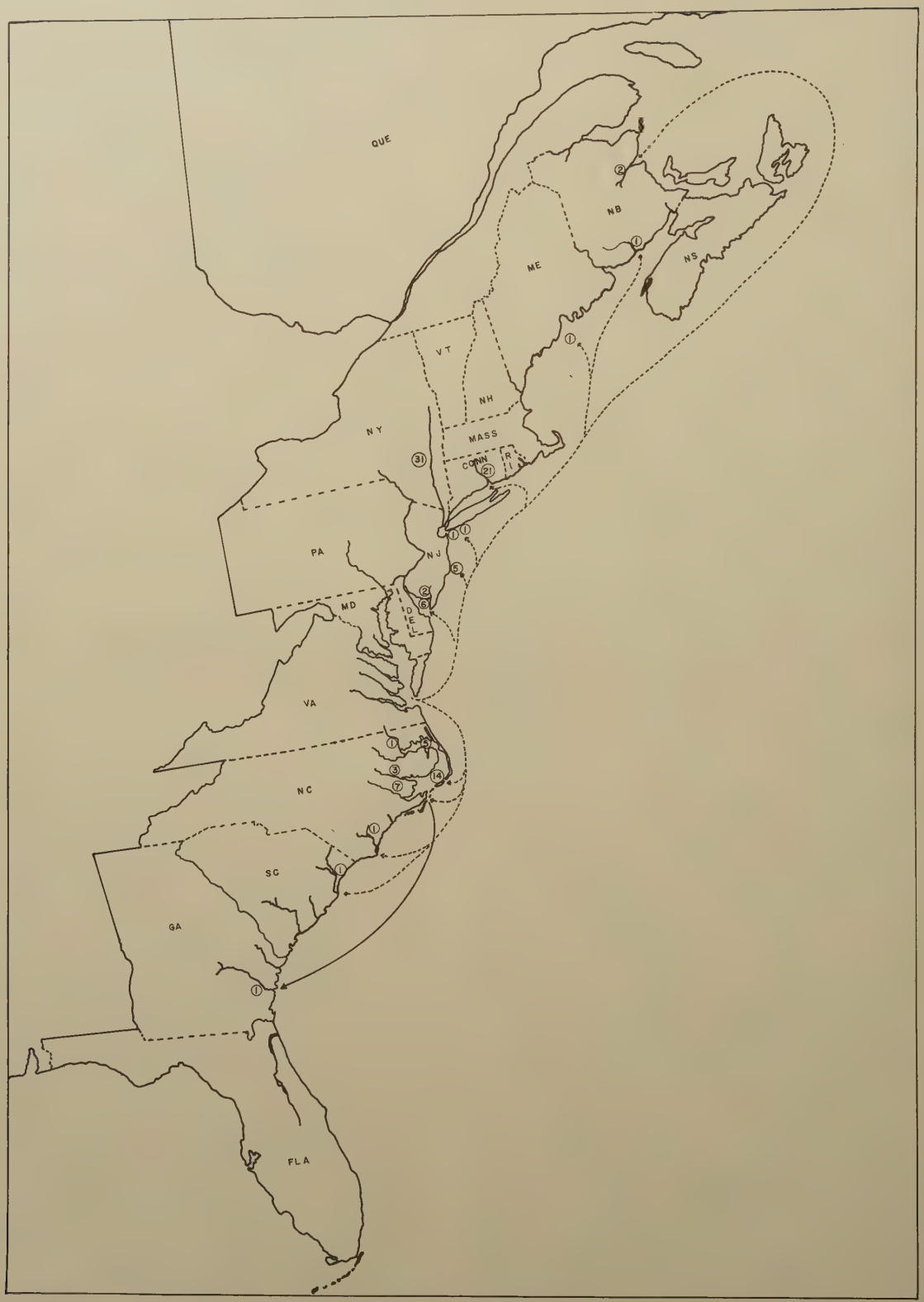


FIGURE 3.—Tags recovered before or during the spawning period (before June 1) affixed in Chesapeake Bay from March through May and at the mouth of the Neuse River from January through April. (The broken lines connect places of tagging with place of recapture, but do not necessarily show the migration route. The figures in circles indicate the number of tags recovered in each locality.)

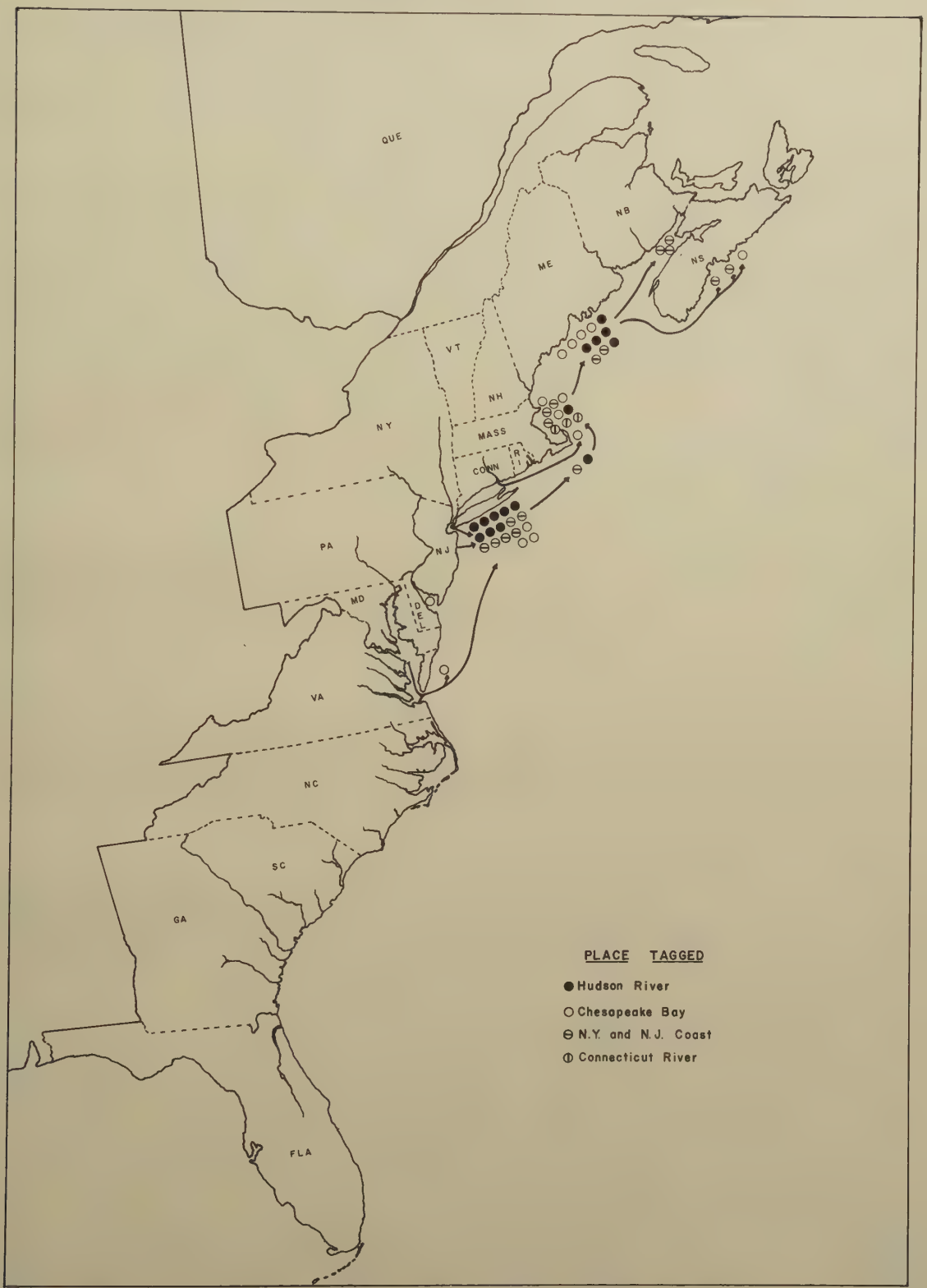


FIGURE 4.—Tags affixed in the Hudson and Connecticut Rivers, off Fire Island, New York, along the coast of New Jersey, and in Chesapeake Bay and recovered after the spawning period (after May 31 south of Long Island and after June 15 north of Long Island).

Very little evidence is available as to where shad spend the winter months. Only one tag was recovered during the period December through January. This fish was tagged in the Connecticut River during the spawning season and recaptured in the ocean off the New Jersey coast on December 13 of the following year. Sometimes when the winter is mild shad in small quantities will enter the sounds of North Carolina during November and December, but will disappear if the weather gets cold. Because shad appear in abundance all along the middle and south Atlantic coast beginning in February, it is assumed that they spend the winter months in this area, probably in deep water.[1]

RECOVERIES FROM SHAD TAGGED IN MAINE

Tagging in the Gulf of Maine was carried out during August and September (table 1) at a time when (as will be shown later) shad are abundant in this area. All the recoveries, with the exception of one tag retaken in November of the year of tagging in Massachusetts, were made the following years during the spring and summer (fig. 5). Most of the recoveries were made south of Maine during the spring in rivers from Georgia to Connecticut. A few were also taken in New Brunswick and Nova Scotia, and in the St. Lawrence River in Quebec during the same period. No Maine tags were recovered from the St. Johns River in Florida, but doubtless shad from this river also summer in the Gulf of Maine during their early years. It seems probable that additional tagging would result in recaptures in this river. If this is true, the early running shad of this river may migrate from the Gulf of Maine directly to Florida, since they enter the St. Johns River as early as November. With one exception, therefore, tag returns indicate that shad from the whole Atlantic coast range of this species can be found during the summer months in the Gulf of Maine.

SPRING RECOVERIES OF SHAD TAGGED ON SPAWNING GROUNDS

Figure 6 shows the tags recovered early in the spring of the years following the tagging of shad on their spawning grounds in the Hudson and Connecticut Rivers. These tag recoveries were made from North Carolina to Long Island during February and March, but as the time of spawning approached, the recoveries were made nearer the mouths of the rivers where the fish had been tagged and to which they were obviously returning. Although tags affixed in the Connecticut and Hudson Rivers were recovered along the Atlantic coast from North Carolina to Long Island, and in Chesapeake and Delaware Bays, not a single tagged fish was recovered from a spawning ground other than the one in which it was tagged. Of the Hudson River tags, 185 were recovered back in the Hudson River, and 23 tags affixed in the Connecticut River returned again to the Connecticut River.

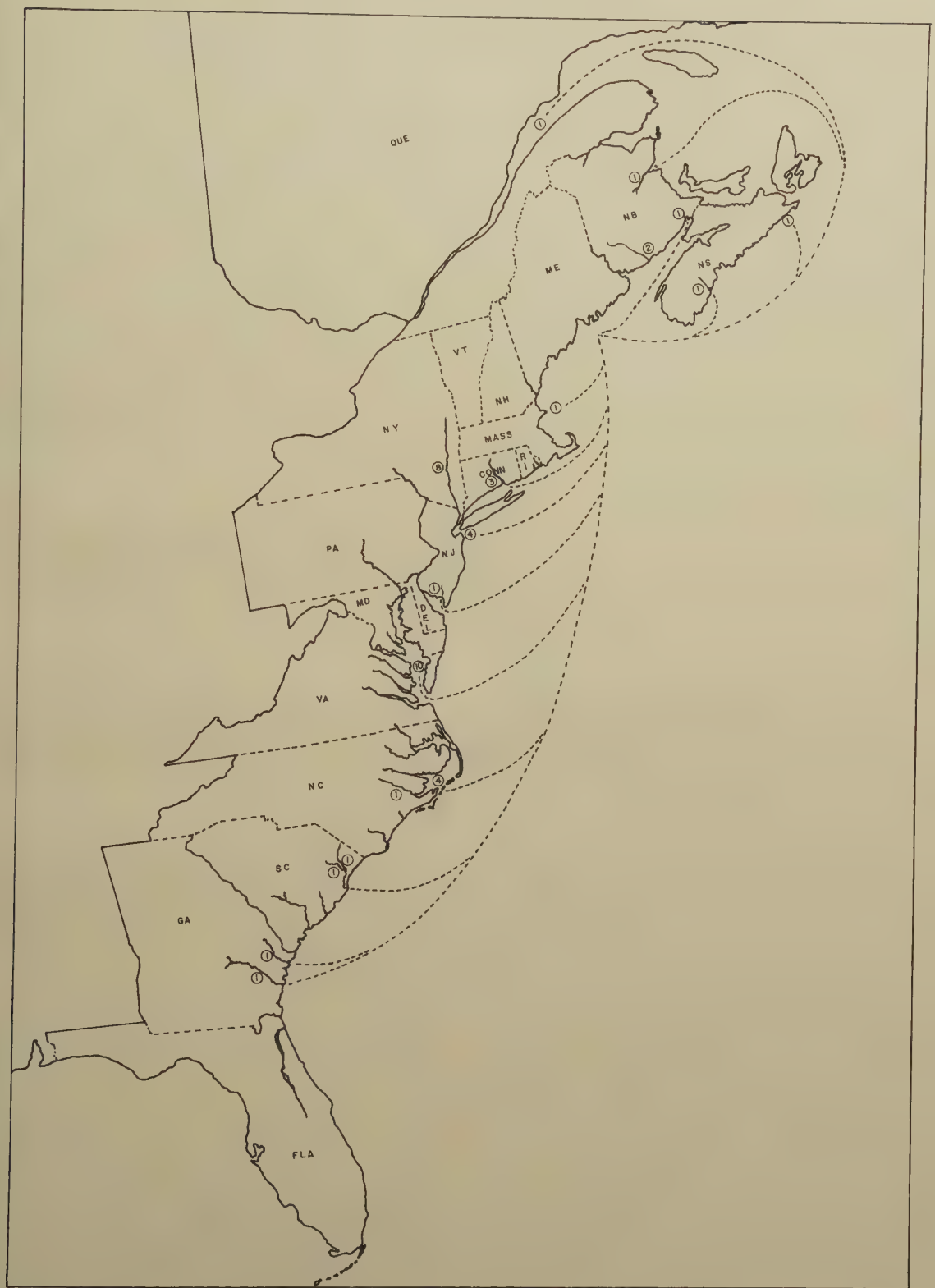
RATE OF MIGRATION OF TAGGED SHAD

The speed with which shad are capable of traveling during their migrations is difficult to determine from tagging experiments, since the routes taken are not known. Furthermore, it is not known how long a shad may have delayed near the tagging site, or how long it may have been in an area before being captured. Table 2 lists a number of recaptures of shad tagged at several locations, and illustrates some of the fastest migrations found during our analysis of tagging data. The distance traveled per day ranged from 14.4

[1] Evidence supporting this theory was obtained on March 3, 1958, when the U. S. Fish and Wildlife Service exploratory vessel *Delaware* caught shad in 40 to 50 fathoms off the coast of North Carolina.

TABLE 2.—*Distance and miles per day traveled by tagged shad*

Place of tagging	Date tagged	Place recovered	Date recovered	Distance (miles)	Number of days	Miles per day
New York: Fire Island	4/18/46	St. John River, N. B	5/27/46	560	39	14.4
New Jersey:						
Beach Haven	5/12/56	Hudson River, N. J	5/17/56	72	5	14.4
Point Pleasant	5/ 5/56	Hudson River, N. J	5/ 7/56	48	2	24.0
Point Pleasant	5/11/56	St. John River, N. B	6/18/56	648	37	17.5
Point Pleasant	4/29/56	Connecticut River	5/ 7/56	192	8	24.0
Seaside Park	4/19/45	Lynnhaven, Va	4/26/45	210	7	30.0
Sandy Hook	4/13/42	St. John River, N. B	5/20/42	576	37	15.6
Virginia:						
Little Creek	4/21/52	Hudson River, N. J	4/27/52	320	6	53.3
Little Creek	4/22/52	Hudson River, N. J	5/ 4/52	320	12	26.7
Little Creek	4/10/52	Neuse River, N. C	4/21/52	260	11	23.6



GURE 5.—Recoveries from the State of Georgia to the Province of Quebec of tags affixed in the Gulf of Maine during August and September.

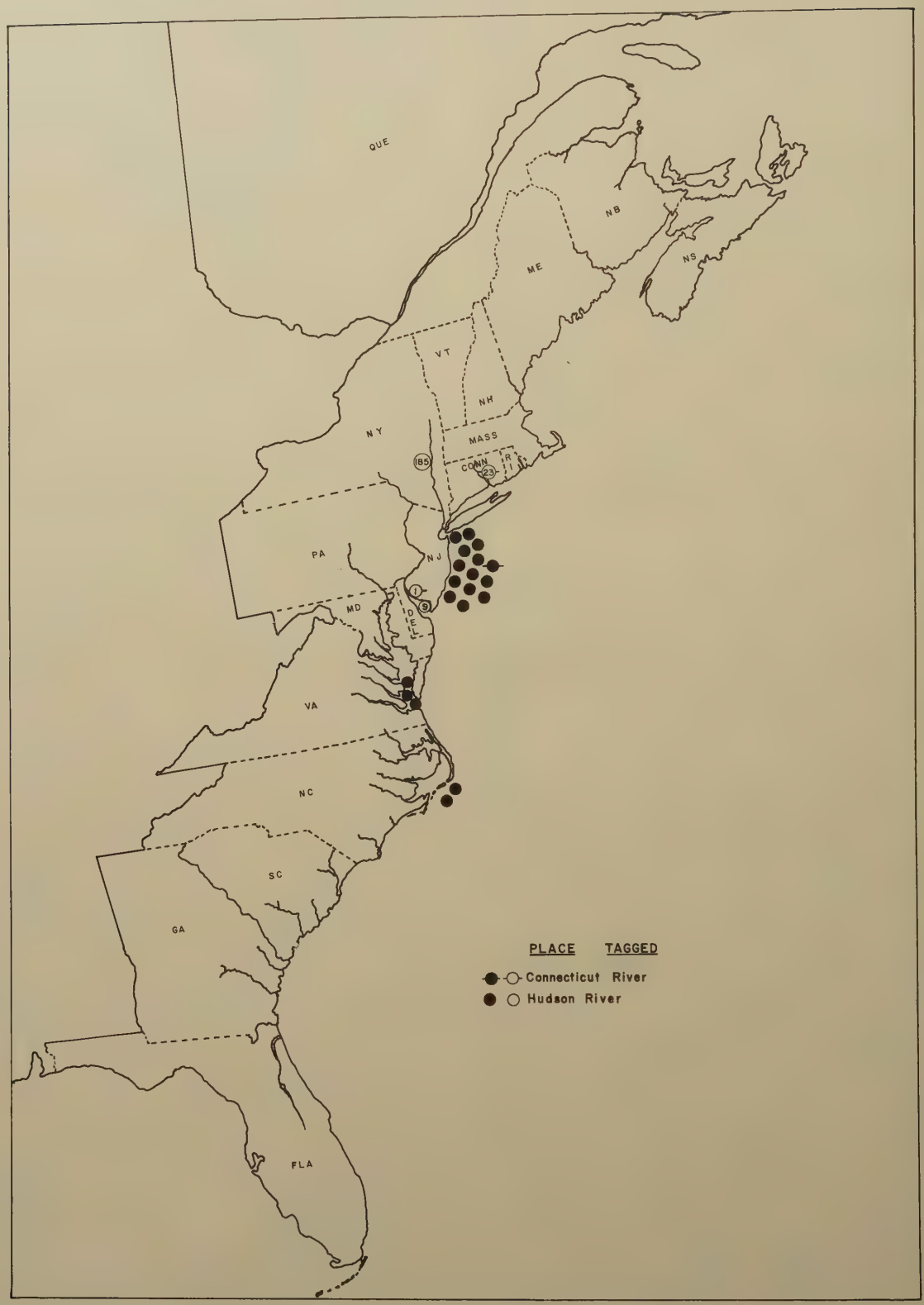


FIGURE 6.—Recoveries in the spring of subsequent years of tags affixed to shad on their spawning grounds in the Hudson and Connecticut Rivers.

53.3 miles. For reasons already given, however, these distances must be considered as the minimum for the individual fish listed.

OTHER EVIDENCE OF MIGRATION

The tag recoveries illustrated in figure 4 show that, after spawning, shad from Chesapeake Bay and the Hudson and Connecticut Rivers migrate to the Gulf of Maine, where they are caught during the summer and fall months. Since there is no reason to believe that untagged shad behave differently than tagged shad, the inference obtained is that untagged shad spawning in streams in Chesapeake Bay and the Hudson and Connecticut Rivers also migrate to the Gulf of Maine after spawning. That this is true is borne out by the large numbers of spent shad that have been reported in the Gulf of Maine since the early part of this century. These were believed to have come from Maine streams, as reported by Bigelow and Welsh (1925: pp. 115–116) who stated that:

> Large spent shad—presumably fish that have spawned in the Kennebec—are regularly caught in September and October about Mount Desert, where they have been the object of a considerable frozen-fish industry of late, as well as near the Isles of Shoals and off York Beach in August, while it has long been known that shad are present 40 to 50 miles at sea off the Maine coast throughout the autumn.

In recent years, shad runs in Maine streams have become almost nonexistent because of dam construction and pollution (Taylor 1951); the same is true of shad runs in the streams of Massachusetts. Yet, large numbers of shad are still found in the Gulf of Maine every summer. Usually, these are not fished extensively for food since they are spawned-out fish and normally bring a low price; but during World War II, when fish prices were generally high and demand was good, a large shad fishery developed. In 1946 over a million pounds were caught—mostly with purse seines (Taylor 1951).

Large shad catches are still made in the Gulf of Maine along with "scrap" fish by boats working out of Massachusetts ports during the summer. Some large catches of "scrap" fish are 100 percent shad, as reported in Massachusetts Fisheries Trends for July 1956 (U. S. Fish and Wildlife Service, 1956: p. 4), "Recent catches of large shad are reported by boats seining for menhaden. Two trips were landed that consisted of pure shad. . . . The two shad trips totaled about 120,000 pounds. . . ." It was reported that other trips brought in mixtures of shad and herring. During the summer of 1957 when menhaden were scarce, menhaden purse seiners turned to shad and landed over 2 million pounds of this species for processing into fish meal and oil.[2] These shad are in such abundance that undoubtedly most of them are from rivers other than those of Maine and Massachusetts, and therefore indicate a migration to this area during the summer months.

It has been shown (Walburg, 1956, 1957; Sykes 1956) that almost all shad spawning in North Carolina and all shad spawning south of North Carolina die after they spawn. This is evident in table 1—no tags were returned after the spawning season from the tags affixed to shad in the streams of these States. Therefore, recovery of Gulf of Maine-tagged shad in southern streams (fig. 5) indicates that these fish must have been tagged as immature shad which moved to the Gulf of Maine area during the summer months and then returned to southern rivers to spawn. This migration to the Gulf of Maine, along with that of immature shad from other Atlantic coast streams, accounts for the large number of immature shad found there each summer as reported as early as 1887 by Atkins (p. 684), who, writing about Maine fisheries, stated, "A more numerous class of immature individuals feed about the bays and in the mouths of the rivers during the summer, later than the ascent of the main body of breeders." Bigelow and Welsh (1925) reported that—

> Schools of small immature shad from a foot long and half a pound in weight up to 2 or 2½ pounds, not yet of breeding age . . . are reported evey year at Provincetown for a short period in June, are sometimes taken in the weirs at Beverly and Manchester in Massachusetts Bay in June, and are met with more or less commonly all summer off Cape Ann and thence eastward . . . .

Later, Bigelow and Schoeder (1953: p. 111) noted that "it seems established that most of the medium-sized shad and larger . . . are immigrants from the south, growing and fattening on the rich supply of plankton they find there, but returning to the rivers west and south of Cape Cod to

[2] In a letter dated Apr. 9, 1958, from Dwight L. Hoy, Commodity Industry Analyst, U. S. Fish and Wildlife Service, Gloucester, Mass.

spawn." Some direct evidence of this was available to Bigelow and Schoeder from preliminary tagging results, which are reported in this paper.

HOMING BEHAVIOR

Considerable evidence is available to show that shad do return to their native streams to spawn. Hollis (1948) released about a thousand juvenile shad, averaging 10 centimeters in length, at Edenton, N. C., in October 1941, after inserting small plastic belly tags into their body cavities. During the spawning migration, 3 to 5 years later, three tags were recovered within a radius of 10 miles from the tagging site. None was returned from any other area.

Later, in a cooperative experiment between the U. S. Fish and Wildlife Service and the Chesapeake Biological Laboratory, Solomons, Md., E. A. Hollis [3] and C. M. Coker [4] inserted 737 belly tags into fingerling shad on October 26, 27, and 28, 1950, and released the fish near the mouth of Mill Creek, which empties into the Patuxent River at Solomons, Md. Four of the tags were recovered 4 years later, three were recovered 5 years after tagging, and one was recovered 6 years after tagging. Three of the tags were returned from dealers and it was not possible to locate their place of capture. Three tags were returned from Chesapeake Bay where the tagged fish could have been on their way to the Patuxent River, and two tags were from Solomons Island. None was recovered from an area which would indicate that the shad might spawn in any place but its "home" stream.

The returns from these two experiments were small, but when the mortality between young and adult stages is taken into consideration and also the fact that small belly tags can easily be overlooked in the viscera of an adult fish, the returns are perhaps all that could be expected. While these experiments do not prove conclusively that shad return to their native stream to spawn, the tag returns, though few in number, suggest that they do.

Hammer (1942) made a study of the scales and body measurements of shad taken in Chesapeake Bay and its tributaries. He used measurements of the fresh-water zone of the scales to compute the juvenile body lengths attained at the termination of the young shads' stay in fresh water. These calculated lengths from various streams differed significantly, indicating that "mature Chesapeake shad return to spawn in the stream of their origin." Otherwise, as a result of intermixing, the calculated lengths would be similar. Other scale characteristics denoted the existence of populations peculiar to each river.

As previously noted, the shad which spawn in streams south of North Carolina die after spawning. No repeater shad were found in samples of scales taken from these rivers and less than 3 percent of the North Carolina shad were found to be repeater fish (LaPointe 1958). In contrast, repeater shad spawning in streams tributary to Chesapeake Bay make up to 27 percent of the population (Walburg and Sykes, 1957) and in the Hudson and Connecticut Rivers up to 50 percent (Moss 1946; Talbot 1954). This is good evidence that little if any mixing or straying of shad of the more northern populations into the populations spawning in southern streams occurs. Otherwise, repeater shad would be found in the southern stocks.

Further evidence that shad return to their home streams to spawn is found in data presented by Fredin (1954) and Talbot (1954). These workers reported, respectively, that 83 percent of the fluctuations in size of run in the Connecticut River and 85 percent in the Hudson River depend upon the spawning populations in previous years. In other words, each of the runs of shad to these rivers is self-perpetuating and fluctuates independently of shad runs in other streams. The Hudson River shad run has reached peaks of abundance twice in the past 50 years (Talbot 1956; unpublished data for 1956) while shad runs of neighboring streams such as those in the Connecticut River have fluctuated independently and in the Delaware River have been at a low level of production during the same period (Sykes and Lehman, 1957). Such variance among streams could exist only if the majority of the shad return to their home stream to spawn.

The only evidence available that might be construed as contradicting the home-stream theory so far as the American shad is concerned is found in the shad transported from the Atlantic coast to the Sacramento River in California and the Columbia River between Washington and Oregon.

[3] Now with Maryland Tidewater Fisheries.
[4] Now with Estacion Experimental Agricola, Puerto Rico.

shad became established in these rivers and soon spread to other streams of the Pacific coast. In this case, however, the transplanted shad did not have their hereditary home stream available to them; hence, if these fish were seeking their home stream, straying might be expected to be a normal occurrence rather than the exception.

The available evidence, therefore, indicates that most Atlantic coast shad do return to their native streams to spawn, and it definitely indicates that shad, having once spawned in a stream, will return to that stream to spawn again if they survive natural and fishing mortalities.

DISCUSSION AND CONCLUSIONS

The recoveries of tagged shad indicate a definite migration pattern with few or no deviations. Occasionally, unmarked shad have been reported in areas that do not conform to the general pattern. For instance, each year in the Connecticut River a number of emaciated adult shad are found in the canal near Windsor Locks during the summer and fall months. It is believed that these fish are trapped in the canal, and remain there until they die or until, by chance, they are carried out into the river during a lockage.

Small numbers of adult shad are also caught each year on eel racks in the upper Delaware River during the summer and fall months (Sykes and Lehman, 1957). Others have been reported in the lower Hudson River during the fall or winter months and they have been reported in Chesapeake Bay almost all through the year. In every instance, however, these shad have been in small numbers and no tags have ever been recovered from them. It must be concluded that these cases are unusual and that the vast majority of the fish follow the migratory pattern shown by the tag returns and the corresponding abundance of shad, as reflected by catches, during this migration.

One factor that might be expected to obscure the recovery pattern of tags and, hence, lead to false conclusions regarding migrations, is the time of year that each type of fishing gear operates in each area of recovery. In other words, tag recoveries might have been made at certain times, only because certain fishing gear was operating at those times. This, however, does not appear to be the case. In Maine, tags were recovered in July through September from operators of purse seines, otter trawls, and gill nets. The purse seines operate from May to December, overlapping the period of shad catches and tag recoveries by at least 1 month before and after the shad catch season. Tags were recovered in Massachusetts from late June to the first week in November. In this State, purse seines operate from late June until October during the time most tags are returned. In both Maine and Massachusetts, otter trawls and gill nets are operated throughout the year but shad are taken in abundance only during August, September, and October,[5] the period in which the tagged shad were caught.

At Fire Island, New York, pound nets have been set as early as March and are in operation throughout the summer and fall until November. A few mature shad are taken here during late March, April, and May, most of which appear, according to tag recoveries, to be heading for the Connecticut River; and spawned-out shad are taken during June. Rarely have shad been caught at any other time of the year.

The pound nets along the New Jersey coast formerly were fished almost all year; some were removed in December or January. In recent years, they have usually been taken up from December through February. Shad are taken in abundance in this area only during the spring spawning run, and it is only at this time that tagged shad have been recovered, with the exception of the one tag taken during December, previously mentioned. In Chesapeake Bay [6] and the bays of North Carolina, pound nets are operated from January through April, and from September through November, but shad, both tagged and untagged, are caught only during the spring spawning run.

In all rivers supporting a spawning run, shad are abundant only during the spawning run and the majority of the shad fishermen set their nets only during this period. In most rivers, however, fishing gear is operated throughout the year for other species, and this would disclose the presence of shad if they were in the rivers in any numbers at a time other than during the regular shad

[5] In a letter dated Oct. 22, 1956, from Dwight L. Hoy, commodity industry analyst, U. S. Fish and Wildlife Service, Gloucester, Mass.

[6] In a letter dated Feb. 11, 1957, from William H. Massmann, Virginia Fisheries Laboratory, Gloucester Point, Va.

season. It appears, therefore, that shad are in abundance only at those places and times indicated by the tag returns and that the pattern of tag return is not the result of peculiarities in the operation of fishing gear.

Returns from shad tagged in the St. Lawrence River by Vladykov (1950) are of interest, since the migration pattern of these fish appears to agree with that indicated by our tagging data farther south. Vladykov found that after spawning shad left the St. Lawrence River during July and August and spent the balance of the summer and fall in the Gulf of Maine. He surmised that they spent the winter and early spring "between the Gulf of Maine and Nova Scotian Banks." However, as can be seen in figures 2 and 3, Canadian-spawned shad are caught as far south as Chesapeake Bay in the spring. In a later paper Vladykov (1957) reports that three shad tagged in the St. Lawrence River during the summer were recovered the following spring in the Middle Atlantic area—one near Old Point Comfort, Virginia; one off Bowers Beach, Delaware; and another off Sandy Hook Bay, New Jersey. It would appear that Canadian shad not only spend the summer months in the Gulf of Maine as do the more-southern spawning shad, but that they, too, spend the winter in the Middle Atlantic area.

We can now conclude from the evidence available that the majority of the Atlantic coast shad make regular migrations each year and return to their native streams to spawn. This pattern has been disclosed by the recovery of approximately 39 percent of the more than 17,000 shad tagged; by the presence at certain seasons of large numbers of immature and adult shad in areas where shad are not natively abundant, and conversely, by the absence of shad in other areas during certain times; and by studies of the scales of shad which have shown that there are separate races in each stream.

In studies of the American shad carried out over a period of 19 years, tag recoveries have revealed a consistent migration pattern, which can be summarized as follows: After spawning, adult shad in streams from Chesapeake Bay to the Connecticut River migrate northward and spend the summer and fall in the Gulf of Maine. Canadian shad migrate southward to the Gulf of Maine and also spend the summer and fall there. There is little evidence as to where shad spend the winter months; but it appears that they are scattered along the Middle Atlantic area, for beginning in January or February as the spawning season approaches, they move inshore and are taken in the commercial fisheries from North Carolina to Long Island. They then migrate either north or south to their native streams and spawn, repeating this cycle each year that they escape natural and fishing mortalities. The young shad leave their native streams in the fall, probably spend the winters in the Middle Atlantic area, migrate to the Gulf of Maine each summer along with the adults, and when mature return to their native streams to spawn. Those that spawn in streams south of Chesapeake Bay, and particularly south of North Carolina, die after spawning.

From these studies it appears that shad, like salmon, migrate long distances in the sea and return to their native streams to spawn. How or by what mechanism they are guided has not yet been satisfactorily determined.

LITERATURE CITED

Atkins, C. G.
1887. The river fisheries of Maine. *In* Goode, G. Brown and associates, The fisheries and fishery industries of the United States, Sect. 5, vol. 1, 808 pp.

Bigelow, Henry B., and William C. Schroeder.
1953. Fishes of the Gulf of Maine. U. S. Fish and Wildlife Service, Fishery Bull., vol. 53, No. 74, 577 pp. [Contribution No. 592, Woods Hole Oceanographic Institution.]

Bigelow, Henry B., and William W. Welsh.
1925. Fishes of the Gulf of Maine. U. S. Bureau of Fisheries, Bull., vol. 40 (1924), Pt. 1, 567 pp.

Calderwood, W. L.
1937. Homing instinct in salmon. Modern skepticism on the homing instinct and the theory of separate races. Salmon and Trout Magazine, No. 88, pp. 207–213. London.

Cating, James P.
1953. Determining age of Atlantic shad from their scales. U. S. Fish and Wildlife Service, Fishery Bull., vol. 54, No. 85, pp. 187–199.

Clemens, W. A., R. E. Foerster, and A. L. Pritchard.
1939. The migration of Pacific salmon in British Columbia waters. *In* The migration and conservation of salmon. American Assoc. Advancement Science, Publ. No. 8, pp. 51–59.

Collins, Gerald B.
1952. Factors influencing the orientation of migrating anadromous fishes. U. S. Fish and Wildlife Service, Fishery Bull., vol. 52, No. 73, pp. 375–396.

AVIDSON, FREDERICK A.
1937. "Migration" and "homing" of Pacific salmon. Science, vol. 86, No. 2220, pp. 55–56.
REDIN, REYNOLD A.
1954. Causes of fluctuations in abundance of Connecticut River shad. U. S. Fish and Wildlife Service, Fishery Bull., vol. 54, No. 88, pp. 247–259.
ASLER, ARTHUR D.
1954. Odour perception and orientation in fishes. Fishery Research Board Canada, Jour., vol. 11, No. 2, pp. 107–129.
ASLER, ARTHUR D., and WARREN J. WISBY.
1951. Discrimination of stream odors by fishes and its relation to parent stream behavior. American Naturalist, vol. 85, No. 823, pp. 223–238.
AMMER, RALPH CURTIS.
1942. The homing instinct of the Chesapeake Bay shad *Alosa sapidissima* (Wilson), as revealed by a study of their scales. Thesis, University of Maryland, 45 pp. [Typewritten.]
OLLIS, E. H.
1948. The homing tendency of shad. Science, vol. 108, No. 2804, pp. 332–333.
UNTSMAN, A. G.
1937. "Migration" and "homing" of salmon. Science, vol. 85, No. 2204, pp. 313–314.
APOINTE, DONALD F.
1958. Age and growth of the American shad *Alosa sapidissima* (Wilson) from three Atlantic coast rivers. American Fisheries Soc., Trans., vol. 87 (1957), pp. 139–150.
EHMAN, BURTON A.
1953. Fecundity of Hudson River shad. U. S. Fish and Wildlife Service, Research Rept. 33, 8 pp.
OSS, DOUGLAS D.
1946. Preliminary studies of the shad *(Alosa sapidissima)* catch in the lower Connecticut River, 1944. Eleventh North American Wildlife Conf., Trans., pp. 230–239.
OWERS, EDWIN B.
1939. Chemical factors affecting the migratory movements of the Pacific salmon. *In* The migration and conservation of salmon. American Assoc. Advancement Science, Publ. No. 8, pp. 72–85.
OWERS, EDWIN B., and R. T. CLARK.
1943. Further evidence on chemical factors affecting the migratory movements of fishes, especially the salmon. Ecology, vol. 24, No. 1, pp. 109–113.
OWERS, EDWIN B., and THRESSA A. HICKMAN.
1928. The carbon dioxide tensions of the Fraser River and its lower tributaries and of certain tributaries of the Columbia River. Puget Sound Biological Station, Publ., vol. 5 (1925–28), pp. 373–380.
ICH, WILLIS H.
1937a. "Homing" of Pacific salmon. Science, vol. 85, No. 2211, pp. 477–478.
1937b. "Races" and "homing" of Pacific salmon. Science, vol. 86, No. 2223, p. 122.
1939. Local populations and migration in relation to the conservation of Pacific salmon in the western states and Alaska. *In* The migration and conservation of salmon. American Assoc. Advancement Science, Publ. No. 8, pp. 45–50.
RUTTER, CLOUDSLEY.
1902. Natural history of the quinnat salmon. U. S. Fish Commission, Bull., vol. 22 (1904), pp. 65–141.
SCHEER, BRADLEY T.
1939. Homing instinct in salmon. Quarterly Review Biology, vol. 14, No. 4, pp. 408–430.
STEVENSON, CHARLES H.
1899. The shad fisheries of the Atlantic coast of the United States. U. S. Commission Fish and Fisheries, Rept. of the Commissioner for 1898, Pt. XXIV, Appendix, pp. 101–269.
SYKES, JAMES E.
1956. Shad fishery of the Ogeechee River, Georgia, in 1954. U. S. Fish and Wildlife Service, Special Scientific Rept.: Fisheries No. 191, 11 pp.
SYKES, JAMES E., and BURTON A. LEHMAN.
1957. Past and present Delaware River shad fishery and consideration for its future. U. S. Fish and Wildlife Service, Research Rept. 46, 25 pp.
TALBOT, GERALD B.
1950. A biological study of the effectiveness of the Hell's Gate fishways. International Pacific Salmon Fisheries Comm., Bull. III, Pt. 1, pp. 1–80.
1954. Factors associated with fluctuations in abundance of Hudson River shad. U. S. Fish and Wildlife Service, Fishery Bull., vol. 56, No. 101, pp. 373–413.
1956. Conservation of an east coast fishery. Gulf and Caribbean Fishery Inst., Proceed., 8th Annual Session (1955), pp. 92–99.
TAYLOR, CLYDE C.
1951. A survey of former shad streams in Maine. U. S. Fish and Wildlife Service, Special Scientific Rept.: Fisheries No. 66, 29 pp.
THOMPSON, WILLIAM F.
1945. Effect of the obstruction at Hell's Gate on the sockeye salmon of the Fraser River. International Pacific Salmon Fishery Comm., Bull. I, 175 pp.
UNITED STATES COMMISSION OF FISH AND FISHERIES.
1898. A manual of fish-culture, based on the methods of the United States Commission of Fish and Fisheries. Rept. of Commissioner for 1897, Pt. 23, Appendix, 340 pp.
UNITED STATES FISH AND WILDLIFE SERVICE.
1956. Massachusetts fisheries trends, July 1956. Boston Fisheries Product Report B-168, August 28, 4 pp.
VLADYKOV, VADIM D.
1950. Movements of Quebec shad *(Alosa sapidissima)* as demonstrated by tagging. Naturaliste Canadien, vol. 77, Nos. 5–6, pp. 121–135.
1957. Distant recaptures of shad *(Alosa sapidissima)* tagged in Quebec. Naturaliste Canadien, vol. 83, No. 10, pp. 235–248.

VLADYKOV, V. D., and D. H. WALLACE.
1938. Remarks on populations of the shad *(Alosa sapidissima)* along the Atlantic coast region. American Fisheries Soc., Trans., vol. 67 (1937), pp. 52–66.

WALBURG, CHARLES H.
1956. Commercial and sport shad fisheries of the Edisto River, South Carolina, 1955. U. S. Fish and Wildlife Service, Special Scientific Rept.: Fisheries No. 187, 9 pp.
1957. Neuse River shad investigations, 1953. U. S. Fish and Wildlife Service, Special Scientific Rept.: Fisheries No. 206, 13 pp.

WALBURG, CHARLES H., and JAMES E. SYKES.
1957. Shad fishery of Chesapeake Bay with special emphasis on the fishery of Virginia. U. S. Fish and Wildlife Service, Research Rept. 48, 26 pp.

WARD, HENRY B.
1921a. Some of the factors controlling the migration and spawning of the Alaska red salmon. Ecology, vol. 2, No. 4, pp. 235–254.
1921b. Some features in the migration of the sockeye salmon and their practical significance. American Fisheries Soc., Trans., vol. 50 (1920–1921), pp. 387–426.
1939a. Psychology of salmon. Washington Academy Sciences, Proceed., vol. 29, No. 1, p. 1.
1939b. Factors controlling salmon migration. *In* The migration and conservation of salmon. American Assoc. Advancement Science, Publ. No. 8, pp. 60–71.

WISBY, WARREN J., and ARTHUR D. HASLER.
1954. Effect of olfactory occlusion on migrating silver salmon (*O. kisutch*). Fishery Research Board of Canada, Jour., vol. 11, No. 4, pp. 472–478.

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